TINBERGEN, N. (1936): The function of sexual fighting in birds and the problem of the origin of "territory". Bird Banding **7**, 1—8.

ULLRICH, W. (1963): Einige Beobachtungen an Wildtieren in Ostafrika. II. Giraffengazellen. Zool. Garten NF **27**; 187—193.

WALTHER, F. (1958): Zum Kampf- und Paarungsverhalten einiger Antilopen. Z. Tierpsychol. **15**, 340—380.

— (1961): Zum Kampfverhalten des Gerenuks *(Litocranius walleri)*. Natur und Volk **91**, 313—321.

— (1963): Einige Verhaltensbeobachtungen am Dibatag *(Ammodorcas clarkei* Thomas, 1891). Zool. Garten NF **27**, 233—261.

— (1964): Einige Verhaltensbeobachtungen an Thomsongazellen *(Gazella thomsoni* Günther, 1884) im Ngorongoro-Krater. Z. Tierpsychol. **21**, 871—890.

— (1968): Verhalten der Gazellen. Neue Brehm-Bücherei No. 373, Kosmos-Verlag, Stuttgart.

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Factors Regulating the Evolution of Microtine Tooth Complexity

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Introduction

As a medium to examine the changes in the last several million years, and as present day indicators of micro-environments, microtine rodents are almost unsurpassed among mammals. Their relative specificity of habitat is a boon to paleoecologists. Also, their rapid evolutionary rate has been and is very important to Pleistocene stratigraphers. Increasing documentation of these changes from the fossil record have made microtine teeth the primary index fossils of terrestrial Pleistocene deposits in both Eurasia and North America (HIBBARD, 1959; KOWALSKI, 1966).

The major changes in the microtines that have been documented from the fossil record mainly involve changes in the cheek teeth. Most discussions about fossil microtines are thus discussions of their dentition. Paleontologists have reached a point where our understanding of the general chronology and highlights of microtine dental evolution is reasonably clear although there are certainly many gaps and many phylogenetic lines yet to be tied. The present study is not an attempt to add new knowledge to either the chronology or the phylogeny of these mice but to examine some aspects of the biology of the dental variations both between taxa and within populations. The nature of microtine dental changes and differences have been touched on by a number of investigators — paleozoologists and neozoologists alike — in connection with systematic, phylogenetic, and dietary studies. I have attempted here to unify some concepts in these fields and intermesh them into a general framework of evolutionary ecology. Among mammals microtines are an optimal group for a synthesis of this type. Microtine teeth were selected as a research medium because they represent an almost unique opportunity to follow well-documented evolutionary changes over a moderately short period of time in the fossil record. Most importantly, a broad spectrum of microtine

species still exists, in the modern fauna, with varied dentitions and in various ecolo-
gical relationships where hypotheses formulated from the fossil lines can be tested, and
analogies can be drawn from comparable conditions of the modern forms.

There are several basic questions generated by a review of microtine dental evo-
lution: why such a rapid radiation, why so much diversity of dental patterns within
the whole group, why the peculiar variations within sub-groups and communities, and
what selection pressures have been responsible for these patterns?

In this paper I have presend several ideas as to why the teeth have evolved the
way they have, and discussed some factors which have influenced these changes. Before
I go into a discussion of the factors which seem to affect the complexity of microtine
teeth, let me briefly review microtine evolution and place the changes in some sort of
ecological setting.

Although the microtines have undergone considerable evolution, it has been within
the narrow confines of the terrestrial „mouse" niches. Only the muskrat *Ondatra* has
switched to aquatic habitat and increased its size beyond the typical microtine range
(aquatic preferences and large size are probably related ecologically or physiologi-
cally). The main changes that the microtines have experienced appear to be dietary.
HINTON (1926) recognized that the living members which have teeth similar to the
early forms are primarily fruit and seed eaters, but most of the recent species prefer
the vegetative parts of plants — the stem, leaves, and roots. The trend toward greater
utilization of the vegetative portions appears to increase throughout the microtine
radiation. This assumption is based primarily on analogies between the diets of modern
forms and the structure of their teeth in comparison to the dental patterns of the fossil
species.

Microtines can be divided on the basis of their dentition into two moderately dis-
crete non-taxonomic categories: those with rooted molars and those with parallel-
sided molars which never form roots. The rooted forms predominated in the Pliocene
and early Pleistocene, and species with parallel-sided molars predominated in the
middle and late Pleistocene. In North America the more common early genera with
rooted molars are *Prosomys, Ogmodontomys, Ophiomys, Cosomys, Pliophenacomys,
Nebraskomys,* and *Pliopotamys.* In Eurasia the common early rooted-toothed genera
are *Dolomys, Mimomys,* and *Pliomys.* No early ancestor has been found which con-
nects the Nearctic and Palearctic species to a stem stock. There are certain similarities
between the New and Old World forms thought to be due to phylogenetic proximity
by European paleontologists and to parallel evolution by American paleontologists
(HIBBARD and ZAKRZEWSKI, 1967). The only genus with rooted molars to have un-
disputed indigenous representatives in both Eurasia and North America is *Clethrio-
nomys.* It has an earlier history in Eurasia and appears to have arisen there. Recently
Pliomys specimens have been found in early to mid-Pleistocene deposits in North-
western Alaska (GUTHRIE and MATTHEWS, unpublished manuscript). Several genera
with parallel-sided molars occur in both Eurasia and North America: *Microtus, Lem-
mus, Dicrostonyx,* and *Lagurus.* All appear to have moderately long histories on both
continents.

Ecologically the present relationships of the rooted to non-rooted forms seem to
follow a pattern seen in other groups (e. g., primates) where the phylogenetic relicts
now occupy special peripheral habitats. Among the living genera with rooted molars
most occupy some atypical microtine habitat. The muskrat *Ondatra* is aquatic or semi-
aquatic. Other groups with rooted teeth are found in arboreal or at least woodland
habitats (e. g., *Phenacomys* and *Clethrionomys*). *Cletrionomys* is very abundant in
some open northern communities but seems to occupy the *Peromyscus*-niche in the
north. *Dolomys* is a nocturnal montaine form and *Ellobius* is extremely fossorial.

The ecological shift from the fruiting part of the plant to the vegetative part resul-

ted in an increasing tooth complexity of which the loss of roots was only one aspect of the change. The enamel perimeter of the crown became extremely convoluted. Each species of recent and fossil microtine has a characteristic molar pattern and there are even gross differences within some species. There is an almost complete spectrum among living microtines representing the different phylogenetic stages of increasing tooth complexity. By combining what is known of the present ecology of the microtine species possessing these different tooth structures with what is known about the evolutionary trends, I believe it is possible to get some insight into what factors now regulate and have regulated microtine tooth shape in the past.

As others have pointed out (e. g., KURTÉN, 1960), the taxonomy of the microtines need revision by someone using consistent standards of species and genera based on variations observed within living communities. I would guess that this will result in greater synonymizing than splitting of taxa. No matter what the changes in future taxonomic revision, the overall direction of the trends is clear, as is our concept of the magnitude of evolutionary rates involved.

Although many authors have referred to the extremely rapid dental changes among microtines, the many different variables involved make it difficult to speak in exact terms of rates of evolution. Taxonomic comparisons of incipient genera or species involve the subjective views of the different taxonomists. Absolute comparisons are impeded by the inadequacies of the fossil record and variations in dating. Some paleontologists feel that such variables as generation length should also enter into any analysis of evolutionary rate. There is also the matter of some major phenotypic changes requiring little genetic change. Therefore, comparisons of similar characters experiencing about the same kind of changes in organisms not too different in generation length or other life history features are more likely to have some validity. Compared to other small mammals, the microtine rodents represent one of the most extreme cases of rapid evolution, both in terms of their rate of phylogenetic diversification and the absolute changes occurring within each line. Other mammalian groups have also had periods of quite rapid evolution, but these radiation bursts for most living mammalian groups occurred in the mid- to late Tertiary. The rapid evolution of the microtines is so apparent because: (1) their major radiation occurred quite late, (2) their fossils are so common (partly because of the high population densities and high rate of turnover), and (3) their wide distribution encompassing most of the Holarctic. Although surely many microtine characters were changing, the rapid evolution of the cheek teeth is probably the most dramatic.

Origin of the trends in microtine molar evolution

As I stressed in the introduction, the main theme governing microtine evolution appears to be the shift from a diet of the fruiting part of the plant to the vegetative portion. At least, the main correlation among the shapes of modern microtine molars appears to correspond with this dietary spectrum. What is most puzzling about the microtine radiation is not that they invaded the grazing niche but that they were so late in doing it. The ungulate lines experienced major changes in the same direction during the mid-Tertiary. It appears that the small-mammal grazing niche went virtually unfilled from the early Miocene to the mid- to late Pliocene. Yet from plant part of the what paleobotanists can gather, there have been no great additions or deletions to the biome structures since the mid-Tertiary. The possible exception, of course, is the development of the tundra. The northern areas may have contained the stem stocks for the microtine radiation producing the disjunct spotty picture of microtine evolution in the American Great Plains and in parts of Central Europe. But still the lack of early occu-

pation by the microtines cannot be explained by the absence of suitable habitat for a small grazer.

If the pre-Miocene plant communities did not include extensive open herbaceous areas, the available habitats could have well been exploited rather thoroughly by mammals such as squirrels and woodland mice eating primarily the seeds (and succulent leaves in season). The holarctic expansion of the temperate northern grasslands, however, opened up immense habitats for those able to survive the whole year on the vegetative portion. The ungulates were in a much closer position to take advantage of this change. The ungulate change from browsing to grazing is major but much less than from a crushingtoothed seed and fruit eater to grass eater. It could be that sheer phylogenetic distance was the most important factor in the evolutionary lag. That is, they were not physiologically, morphologically, etc., capable of taking full advantage of the expanding grasslands. The fact that the microtine evolution has been so rapid and yet microtines were apparently not able to fill the grassland niche for quite some time also argues for the lack of phylogenetic proximity idea. Actually the evolution of another group of grazers, the mammoths, also lagged behind the development of the grasslands, probably for similar reasons.

The main trends in the microtine dentition relate to two main themes: a. a more complex grinding surface on the crown and b. a. prolonged resistance to a functional reduction of the crown by abrasion.

The trends involved in the first of these two interrelated categories may be characterized by 1. an increase in the degree of penetration of re-entrant angles, 2. an increase in acuteness of salient angles, 3. a decrease in width of re-entrant angles, 4. the addition of salient angles to the posterior end of the uppers and the anterior of the lowers, 5. an increase in the degree or alternation of salient angles, 6. the re-entrant angles of the uppers increase in the degree of posterior alignment and lowers anterior, 7. an increase in specialization of enamel, thick anterior surface of salient angles of uppers and posterior of lowers, and a thinning of the enamel on the apices of the re-entrant and salient angles.

In the second category there are trends toward: 1. an increase in hypsodonty, 2. a reduction in the number and size of the roots, and, finally, 3. the development of continuously growing cheek-teeth. Superimposed on these different trends is the acquisition of cementum in the re-entrant angles in several lines. There seems to be no general trend in absolute size of the molars. With but a few exceptions the microtines have varied within narrow size limits. HIBBARD (1964) and other authors have referred to these trends and listed additional ones, such as the elongation of the lower incisor HIBBARD has on a number of occasions pointed out that these trends do not necessarily all exist concurrently in different microtine lines, nor at the same rates, nor even in the same sequence. In spite of this fact, the changes seem to be related as part of the same syndrome of changig to a more abrasive diet.

The different evolutionary trends found in the microtines are in actuality the same trends one sees in any grazing radiation, i. e., an increase in tooth height (hypsodonty) to compensate for increased crown attrition, and increased crown complexity of the enamel to increase the masticatory efficiency by increasing the amount of the cutting edges. The two are interrelated, as a complex crown should also decrease the rate of wear. The microtines differ from many other grazers in their mode of jaw movement. They have a high antero-posterior (propalinal) component to their jaw movements, as can be seen in the abrasion scratches on the enamel. As a result of the anterio-posterior jaw motion, the thicker enamel of the later microtines is at right angles to the siggital plane. Those enamel areas that are almost parallel with the saggital plane are thin or deleted all together. These areas are the medial parts of the re-entrant angles and the outermost apex of the salient angles.

Another unusual feature of the microtine evolutionary pattern is that there are very few groups of mammals that have had their major radiation at high latitudes. Today most mammalian groups have their concentrations of genera to the south. Microtines, therefore, represent a reversed taxa cline. The number of microtine genera is greater in the Arctic and Subarctic and, for the most part, declines toward the equator. With the exception of the microtines, the Pleistocene and Recent mammal communities in the north are made up of a hodge-podge of representatives from more southern radiations.

Kurtén (1960) has pointed out that the changes within the microtine radiation are unidirectional rather than fluctuating. When the different evolutionary lines are examined in detail, there are some exceptions to this statement, but on the whole, he is correct. Any one of the indices of tooth complexity plotted for Pleistocene voles and lemmings illustrates this directional increase in tooth complexity.

Increasing tooth complexity has taken place both at the level of the new lines which originated by speciating, and in old lines which are physically evolving. There are some lines, however, which are moderately stable. In addition to these early lines, which have not changed appreciably, there are also new groups which have recently invaded niches which were once occupied by older lines that have since become extinct. The diversity of the community has an additive character.

This pattern is different from some radiations in which all lines are moving (although perhaps irregularly) toward a certain morphology that can best utilize a new habitat. The microtines generally maintain the whole spectrum of morphological tooth types, seldom eliminating the few most "primitive" tooth forms in the community. I should emphasize that this is an ecological or community phenomenon more than phylogenetic. Almost all microtine lines show some tendency to move toward the high and complex crowned tooth form. However, many lines do leave evolutionary relict branches behind, representing the more original simple crown form. *Microtus* is an excellent example of this phenomenon within a genus. The general trend within the genus *Microtus* has been to increase crown complexity (Guthrie, 1965). Many species, however, have simple tooth shapes not too dissimilar from their early Pleistocene ancestors. From what we know now of the history of microtine communities, it appears to be a phylogenetic tangle with different possibilities along in the continuum of increasing tooth complexity being pre-empted and sometimes retaken by different phylogenetic lines. In one community it is one genus that occupies the most complex dental from in the community; at another time or place it is another genus. The same is true for the forms with the least complex teeth.

The trend to increase tooth complexity is only an overall phenomenon. When phylogenies are examined in detail, there are many evolutionary "flat spots" and even reversals, as I will discuss later. The overall trend, however, in increased tooth complexity is indisputable. The trends within each line can be understood best if one keeps in mind the evolution of the whole community. The microtines in essance had only one available route in which to radiate, that is, *away* from the Cricetinae. If the small mammal herbivore niches could be illustrated in a tier (Fig. 1), with the fruit and seed eating positions at the bottom and the grazing ones at the top, it is easy to see how the microtine dietary radiation almost had to be directional. Since those positions near the base line were already occupied, an increase in community complexity could mainly occur toward the grazing end of the spectrum. It appears that competition then forced an expansion of most new branches into the only available route, a coarser diet of leaves, stems and roots. These latter opportunities increased with the expanding grasslands. What surely happened was that the new phylogenetic lines which were able to capitalize on the vegetative portions were able to persist alongside the fruit and seed eaters; whereas those new lines that utilized the fruit and seeds either never
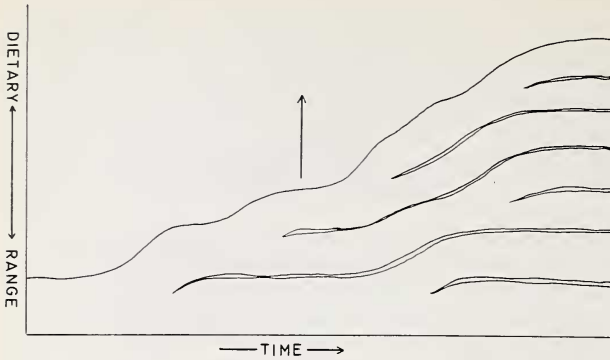
DIETARY ← → RANGE

——TIME——→

Fig. 1. Schematic diagram of the nature of microtine dental radiation in relation to diet. The higher tiers represent exploitation of a more abrasive diet (roots, leaves, stems, etc.). The lower tiers represent a more fruit-seed type diet.

occurred or could not compete with the resident fruit and seed eaters and became extinct, or they were able to replace them, which essentially produced no ecological change in the community structure.

The community evolution in microtines is doubtless more complex than the theory illustrated by Fig. 1. Viewed in its multidimensional form, the small mammal community has many possibilities for increases in complexity without radical change in dietary preferences, such as specializations for woodland vs. open meadow, terrestrial vs. aquatic or arboreal, large size vs. small size, etc. However, this does not negate the theory, it only points out the incompleteness.

Selection pressures affecting microtine tooth complexity

If the theory presented in the foregoing section is correct that the evolutionary radiation of microtines is an increasing exploitation of the newly abundant herbaceous vegetative plant parts as a result of other niches being occupied, it seems likely that *the selection pressures governing tooth complexity within any line are determined, or at least directed, by a combination of the nature of the community structure and the potential opportunities for diversification.*

Since it is almost impossible to measure existing selection pressures directly, one can only analyze the pattern of the changes that have taken place in comparison to the different circumstances involved and assume, with good reason, that natural selection has been responsible. Given a certain community structure, one should be able to predict the relative degree of stabilizing or directional selection pressures which exist (or, in reality, have existed) and be able to test this prediction by analyzing the nature of the species variation. Since intensity of stabilizing pressures or (thinking of it in another way — niche width) should correspond to the expressed variation, as others (VAN VALEN, 1965; SELANDER, 1966) have shown. The more intense the stabilizing pressures (the smaller the niche) the less expressed variation one would expect to see. The existence of directional selection for any length of time should be easy to detect, simply as some sort of selection response — that is, a change in the mean.

If most of the selection pressures on microtine tooth complexity came from competition with other members in the community, one could formulate several expected results or rules — all else being equal — governing microtine evolution.

1. Species living in more complex communities should have less variable teeth than those species living with no sympatric competition.
2. Species with the most complex teeth should be evolving (or have evolved)) at a faster rate than other members in the community (that is, they should be experiencing greater directional selection pressures since they are the lines most likely to move farther into the unexploited grazing niche).
3. Species with complex teeth, from a heterogeneous microtine community, that are placed

alone on an island with varied plant types should experience a change to a simpler denti-
tion. The reverse is true for a simple-toothed form.

4. If a species (A) with simple teeth comes into greater competition with another with more
complex teeth (B), in part of its range one can expect that A will have even less complex
teeth in the area of greatest competition, and B to have more complex teeth.

5. If two habitats (say woodland and meadow) are partitioned between two different species
with little overlap and one species should be removed, the other could be expected to
invade that habitat and extend its range of dental complexity toward that of the displaced
species.

6. When two species live sympatrically in the same micro-environment, the complexity of their
dentition will not be the same, i. e., the phenomenon known as *character displacement*
(WILSON, 1956).

7. A heterogeneous microtine community should represent the broad spectrum of tooth com-
plexity.

Before going into individual cases of competition between specific microtine species
and genera, we might first take a brief look at a microtine community to compare the
model with a real situation. In Fig. 2 I have given a rather stylized illustration of the
diets (and, accordingly, tooth complexity) of the principal microtines in Alaska. These
are the microtines with which I am most familiar. No specific analysis has ever been
made on the ecological roles of all Alaska microtines, although there are several sum-
maries which deal with parts (BEE and HALL, 1956; PRUITT, 1966; RAUSCH, 1951;
PITELKA, 1957; and GUTHRIE, 1969). In some areas where the vegetation or micro-
environment is very homogeneous, only one or two species can be found, but in most
situations there are more than one or two species even though one may be dominant. In
these northern species, drainage (or the amount of moisture) is an important element
in their ecology. Thus, I have used it as the other axis in Fig. 2. The two-factor separa-
tion does not do justice to the many other things that govern microtine habitat pre-
ferences, but it does illustrate some basic differences which will suffice for our purposes
of discussing tooth complexity.

The spread of the different species cannot be illustrated well in Fig. 2, but one can
see that the preference
peaks scatter throughout
the possible habitats. *Cle-*
thrionomys, which has the
least abrasive diet, occu-
pies one end, primarily
the woodland, but is al-
most ubiquitous wherever
overhead cover exists.
Lemmus and *M. oecono-*
mus occur in primarily
moist places, although
Lemmus is more of a gra-
zer. *M. pennsylvanicus*
and *M. longicandus* oc-
cupy moderately well-
drained-to-moist areas
and are primarily gra-
zers, while *M. gregalis*
(= *M. miurus*) is found
almost always in quite
well-drained areas, usu-
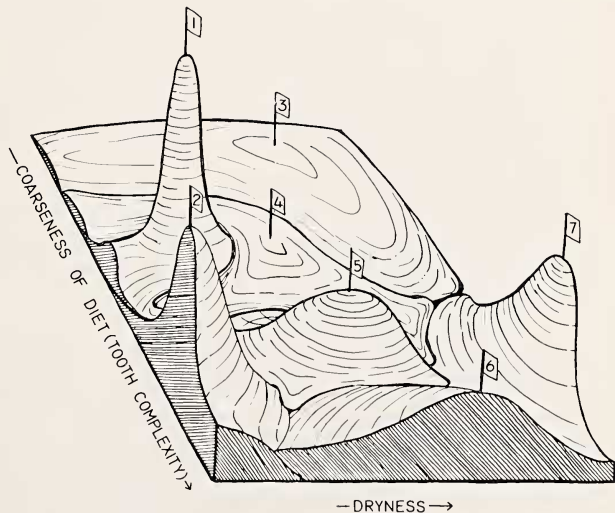ally on alpine slopes.
Dicrostonyx has the most

Fig. 2. A diagramatic illustration of the dominant microtines
and their habitats in Alaska on two parameters. The species
are 1 *Lenimus lemmus*, 2 *Ondatra zibethica*, 3 *Clethrionomys
rutilus*, 4 *Microtus oeconomus*, 5 *Microtus pennsylvanicus*,
6 *Dicrostonyx torquatus*, 7 *Microtus gregalis*

complex teeth and apparently the most abrasive diet and occurs in varying conditions, but seems to prefer the drier areas. Taken together with the other variables in microtine ecology, the peaks of dietary preference seem to be dispersed in an equidistant pattern; which is consistent with what we would expect from the model of microtine community evolution.

Now, jumping from the community to the more specific comparisons, we can look at what has happened to tooth patterns in different individual cases of microtine competition. I have separated the types of competition into several categories, which are purely operational, for discussion purposes only. These are: competition between species, competition between different microtine genera, competition with nonmicrotines, and, finally, isolated species with no intergroup competition.

Competition between species of the same genus

At least three potential expressions of competition between species exist (1) allopatric complementarity (where one species geographically replaces another species with a similar habitat preference) in their geographic distributions, (2) sympatric complementarity (where the preferred habitats, although both are in the general area, are separated ecologically, physically, or in other ways), and (3) the situation where both sympatric species actually do occur in the same microenvironment but have complementary specialization produced by their competition. The second and thrid categories are rather similar, since they represent the two extremes of a continuum, so my examples will refer to both.

There are numerous examples of the first case. The two abundant species of the genus *Clethrionomys* in North America *(C. gapperi, C. rutilus)* have somewhat similar tooth complexities and are complementary in their distributions. Distributions of Eurasian species of *Clethrionomys* are also complementary. *C. rutilus* occurs primarily in the north and *C. glareolus* in the south. It appears that the absence of *Apodemus* is necessary for both to co-exist extensively (CORBET, 1966). *Apodemus* is even less of a grazer than *Clethrionomys,* so perhaps its absence provides greater niche width allowing two species of somewhat similar habits to co-exist.

The bog lemmings, *Synaptomys cooperi* and *Synaptomys borealis,* are essentially mutually exclusive in their range (HALL and KELSON, 1959). *Dicrostonyx torquatus* and *Dicrostonyx hudsonius* also do not overlap geographically; also *Phenacomys intermedius* and *P. longicaudus.*

Among the species of the genus *Microtus* there are numerous examples of allopatric complementarity and, thus, presumably competitive exclusion. CORBET (1966) points out this type of relationship between *M. agrestis* and *M. socialis* and between *M. nivalis* and *M. oeconomus* in Europe. In North America *M. montanus* and *M. californicus* also show this relationship.

There are several studies that provide us with evidence of interspecific competition between sympatric species. A few examples will illustrate how these relate to tooth complexity. ZIMMERMAN (1965) analyzed the preferred habitats and stomach contents of two sympatric species of *Microtus.* He found that *M. pennsylvanicus* occurred predominantly in fields containing at least 50 % grasses with abundant cover, whereas *M. ochrogaster* was found in areas with fewer grasses and less cover. The latter had a broader dietary variety than *M. pennsylvanicus.* The teeth of the two species are quite different. Those of *M. pennsylvanicus,* like a true grazer, are much more complex. The teeth of *M. ochrogaster* are among the simplest found in the genus. They are more similar to *Clethrionomys* or other microtines with more varied menus. FINDLEY (1954) has also suggested that competitive exclusion serves to maintain the separation of these two *Microtus* species in situations of sympatry.

The two species of *Microtus* that are most abundant in the north, *M. gregalis* (= *M. miurus*) and *M. oeconomus,* show much the same sympatric complementarity (Pruitt, 1966). *M. gregalis* is usually found in drier, welldrained sites that usually correspond to the grassy alpine meadows, while *M. oeconomus* is found mostly in the moist lowlands. In some areas populations are contiguous. *M. gregalis* has the more complex dentition. In interior and parts of southern Alaska *M. pennsylvanicus* has pushed northward since the opening of the Cordilleran corridor since the last glaciation (Guthrie, 1969), and now occupies some of the same areas as *M. oeconomus.* Where the two occur together I have noticed a similar separation into two different habitats.

Character displacement within *Microtus* is so general that one could say that where two *Microtus* species occur sympatrically seldom do both have dental batteries of similar complexity.

Two species of *Clethrionomys* are spread over the northern parts of Europe and Asia. *C. rutilus* has more complex teeth than *C. rufocanus.* and the two are frequently sympatric (Corbet, 1966). Farther south there is only one species, *C. glareolus,* which has quite variable teeth (Ibid.).

Koplin and Hoffman (1968) illustrated that habitat segregation in sympatric population of *M. pennsylvanicus* and *M. montanus,*is due to competitive exclusion by experimentally removing individuals of *M. pennsylvanicus* which resulted in enroachments of *M. montanus* into the area.

Competition between Genera

There is some direct evidence of intergeneric competition among microtines (Chitty and Phipps, 1966). However, the best indirect evidence of competition between genera of microtines comes from island populations. The severity of competition between the two most common microtine genera, *Microtus* and *Clethrionomys,* on islands has been presented by Cameron (1964). He found that once a small island is colonized by one species of either genus it will exclude a species of the other. Although both genera occur on the offshore islands of Great Britain, some are inhabited by *Clethrionomys* and others by *Microtus,* but on none of the offshore islands do they occur together. There are several pairs of ecologically similar islands, one of which is inhabited by *Microtus* and the other member of the pair by *Clethrionomys.* Cameron suggsts that the most likely explanation for this phenomenon is that the first genus to reach an island can prevent further colonization, rather than the species being on the island because it is better adapted to the island condition than other forms. Cameron also found that on some wooded islands in North America, *Microtus* appropriates the ecological niche of *Clethrionomys* and occupies the woodlands, which it normally shuns on the mainland.

These island situations provide us with some information of the nature of the habitat competition on the mainland and how it relates to tooth morphology. Where *Clethrionomys* occurs on an island uninhabited by *Microtus,* its teeth tend to become more complex; however, where *Microtus* is found on an island uninhabited by *Clethrionomys,* it generally has less complex teeth than its counterparts on the mainland. On the islands of Ramsay, Jersey, and Skomer in Great Britain, where no *Microtus* are found, *Clethrionomys glareolus* has a large fourth inner ridge on the M^3, whereas on Mull and on the British mainland, the inner ridge is small (Corbet, 1964). *Clethrionomys* shares these latter two places with *Microtus argrestis.*

St. Matthew, a small island on the Bering-Chukchi platform between Alaska and Russia, is inhabited by a species of *Microtus* which has apparently been derived from the Holarctic *M. gregalis* (= *M. miurus*) (Rausch and Rausch, 1968). Since St. Matthew Island was part of the land bridge during the Wisconsin glaciation

(HOPKINS, 1959) it is probable that this species, *M. abbreviatus*, has undergone very rapid evolution since the inundation of the Bering-Chukchi land bridge. The most striking difference between the St. Matthew Island species and the *M. gregalis* on the mainland is in the simpler and more rubust teeth of the former. *M. gregalis* shares the mainland with other species of *Microtus* and other genera of microtines. Among these other mainland forms it has quite complex teeth. Thus, one would have predicted that without the competition from this mainland microtine community, *M. gregalis* would exploit a broader food resource and, as *M. abbreviatus* has done, reduce its tooth complexity.

Island situations seem to increase the competition which the species are adapted to on the mainland. Small offshore islands seldom, as CAMERON (1964) pointed out, hold two species of microtines. On the other hand, St. Lawrence Island, a much larger island just north of St. Matthew, has three species of microtines. Islands the size of Scotland and England seem to be well above the critical size which will allow more than one species of vole in a confined situation.

There also appears to be competition between *Peromyscus* (a non-microtine) and *Microtus*. Although *Peromyscus* has colonized the Queen Charlotte Archipelago in eastern Canada, *Microtus* has failed to do so (FORSTER, 1963). Increased competition in a more restricted area, or more homogeneous one, is probably a general phenomenon.

The two northern Lemmings, *Lemmus* and *Dicrostonyx*, usually occur together. Although they differ in microhabitat preferences, *Dicrostonyx* is more likely to occur with *Lemmus* than with any other microtine (PRUITT, 1966). Wherever the two genera occur, *Lemmus* seems to be dominant. Actually, *Dicrostonyx* is seldom dominant in any microtine community. The fossil record of these species is sporadic but sufficient for us to see the *Lemmus* molar pattern has remained almost unchanged, while *Dicrostonyx* has been rapidly increasing the complexity of its molar pattern. It is perhaps more than coincidental that the only major area in the *Dicrostonyx* distribution where *Lemmus* is absent is where *Dicrostonyx* retains an earlier simpler tooth pattern. This area is on the Hudson Peninsula, and the species is *Dicrostonyx hudsonius*. I suspect that the increase in *Dicrostonyx's* tooth complexity was a gradual invasion of a dietary from that reduced its competition with *Lemmus* and the northern *Microtus* species. In an area where *Lemmus* was absent, such as the Hudson Peninsula, *Dicrostonyx* might not be subjected to as great a competition pressure to increase tooth complexity. (The large *Dicrostonyx* living on some Aleutian Islands [Umnak] are in an unusually grassy northern environment.)

The Vegetational Component

Although competition from related species or other taxa is very important in regulating microtine tooth complexity, there is another factor that cannot be ignored. This is the simple direct relationship to the vegetation. If for some historical reason a species existing without competition from outside subsists on a plant species or series of species that have become only a minor part of the local vegetation and there are other edible but quite different plants predominating, it is reasonable to assume that individuals who can utilize these abundant plants will be able to make a greater genetic contribution of future generations. That is, the species will adapt to the new vegetation.

The best examples of this phenomenon again come from insular situations.. I mentioned earlier how *M. gregalis*, when isolated on St. Matthew during the last glaciation, away from any other microtine, changed its teeth, as well as other characters for that matter, to such a degree that it has been considered a completely different species (RAUSCH and RAUSCH, 1968). *M. guatamalensis* and *M. umbrosus* exist in „ecological

islands" on isolated mountain peaks and are quite different than related species who share their habitats with other taxa. *M. breweri* and *M. nesophilus* are insular species and have simpler tooth crown patterns than their „parent" species, *M. pennsylvanicus*, on the mainland that shares its habitat with *Clethrionomys*.

There is inferential evidence that the selection pressures exerted by the vegetational patterns differ between areas even with the same microtine community. There is a general cline in England from north to south in tooth complexity in both *Microtus* and *Clethrionomys*. The races on the island of Mull, which also has both *Microtus* and *Clethrionomys*, tend to have simpler teeth than the other islands that have either *Microtus* or *Clethrionomys*.

CORBET (1963) studied two populations of *Clethrionomys glareolus* in two different adjacent habitats and found that the two differed greatly in tooth complexity. The one with the simplest tooth crowns lived in an older conifer, beech, and sycamore planting while the adjacent population (less than a quarter of a mile away) had very complex teeth and lived in a new planting recently dominated by young shrubby vegetation. Unless one wishes to invoke „genetic drift" it seems likely that the dental differences are a product of the differences between the vegetational substrates.

Selection Pressures and Tooth Variation

From an evolutionary viewpoint, one of the most interesting characteristics of microtine teeth is the pattern of dental variation within populations. Although the molar row is a highly organized and an integrated complex series of opposed slicing blades, some teeth (and parts of teeth) exhibit almost no intrapopulational variation while other teeth (and tooth parts) are extremely variable. I discussed, in an earlier study (GUTHRIE, 1965), the definite pattern of these differences in amount of variation. The teeth and tooth parts which have evolved most rapidly are the most variable, while those teeth, and parts of teeth, which have remained much the same for a long period of time exhibit the least variation. This finding contradicts the usual assumption that rapidly evolving characters are not prone to show much intrapopulational variation.

When the above two pieces of information (the pattern of the dental evolution as seen from the fossil record and the pattern of morphological variation of individual teeth and tooth parts within modern populations) are placed with the ecological and zoogeographical information about modern species (competitive exclusion, clines in tooth complexity, habitat preferences, and intracommunity relationships), it precipitates a more satisfying picture of microtine tooth variation than one can get by looking at the three different aspects separately.

There are at least three main things about microtine tooth variations that have to be explained: 1. the pattern of tooth evolution (why some teeth and tooth parts should evolve differently than other adjacent ones); 2. the pattern of intrapopulational variation (why some teeth and tooth parts should be much more variable than neighboring teeth); and 3. the pattern of interpopulational difference (why the populations in some situations have different types and amounts of variation than other populations of the same species). Each of the three approaches can contribute to an understanding of the other two.

We have seen that community competition--that is, between species and genera, and to some extent with other non-microtines--can influence the directional and stabilizing selection pressures acting on the teeth. If a species is without competition, it tends to move towards an optimum where it takes advantage of the major vegetation type. Also, it tends to utilize a wide range of available vegetational types, since no competition exists; thus, the microtine population is more variable. In situations where the

stabilizing pressures are more intense, intrapopulational variation is less (as in the case of one species living in a complex community where the outer range of possible habitat and food shared with a number of different species). The nature of this competition has also influenced the orientation of the directional selection; since one end of the continuum of food types was already occupied, radiation could go only in the other direction.

The different evolutionary rates in different parts of the tooth row are to some degree related to the different patterns of intrapopulational variation. With the first forms of the characteristic microtine molar loop followed by alternating triangles, the future range of variational possibilities was determined. A relaxed stabilizing selection pressure would be bound to result in an increase in variation at the end farthest from the loop, since the addition or deletion of enamel convolution is physically more difficult at that end. The variational gradient both within and between teeth is thus directed toward the anterior in the lowers and toward the posterior in the uppers (GUTHRIE, 1965). Once the differences, even though slight, in variation have been established, and are heritable, there would be a greater likelihood that directional selection would produce a change in the more variable areas first. Consequently, increases in tooth complexity have occurred in M_1 and M^3 most commonly. When changes do occur in the other teeth, it is on the posterior parts of the uppers and the anterior parts of the lowers. Each species has this general pattern of variation. Differences in jaw mechanics must also play some role. The decline in complexity of the *Microtus* M_3 (GUTHRIE and MATTHEWS, unpublished manuscript) can probably be explained by the posterior restriction (and isolation from the other two molars) from the unusual position of the incisor root in this genus.

The dental morphology is directly tied up with the demands of the diet; thus, teeth seem to be a sensitive indicator of significant dietary shifts. Not only is the mean dental complexity of a species an indicator of the nature of recent selection pressures, but the relative amount of variation should be, at least, an indicator of the recent intensity of stabilizing pressures (exerted by either the community or the vegetational composition).

The model (actually models) presented here to explain the intraspecific and interspecific differences rely on the variations being heritable. By examining pedigrees of *Clethrionomys* (STEVEN, 1953), and *Microtus agrestis* (ZIMMERMAN, 1956), it has been concluded that the variations of M^3 are genetically controlled by an incomplete monofactoral element. Although mammalogists often refer to the molar variation as *simplex* or *complex* types, the variation spectrum is continuous. With this in mind, I ran a heritability experiment to see how much additive genetic variation existed. The tundra vole, *Microtus oeconomus,* was chosen because of the accessibility of a laboratory colony. This species is intermediate in the degree of dental complexity when compared to the various other species of *Microtus*. The original colony was started from wild animals from Fairbanks, Alaska. The heritability estimates for the dental measurements are given in Fig. 3. Unfortunately, the errors of the estimates are rather high--too high to come to any definitive conclusions about the comparative aspects--although some patterns do seem to exist. The more phenotypically variable areas (M_1 M^3) have lower heritability estimates. The general magnitudes seem to be lower than found in similar studies of teeth from other taxa (BADER, 1965; LEAMY and BADER, 1968). This low variability may correspond to that found in nature or it may be a result of the uniqueness of the sample. The latter is more likely. The colony was kept by the Institute of Arctic Biology for studying several physiological parameters of response to cold stress. I used specimens that died naturally or were sacrificed in experiments. A son-sire regression was made, as this eliminates some variables that other techniques of heritability estimation do not (see FALCONER, 1960, for a review of the procedures). At the start of the colony, detailed records of offspring were not kept, to the amount of inbreeding

cannot be estimated--but there assuredly has been a moderate amount. Because the mice were used for. multiple purposes (subjected to stresses and administered medications) before I worked with them, the heritability estimates are probably lower than what one would find if these variables were eliminated.

Despite the high standard error and the possibility that the estimates are low, they do illustrate the existence of a heritable additive fraction of the observed variation.

Fortunately, we have just discovered (GUTHRIE and MATTHEWS, unpublished manuscript) a species that is doubtless the ancestor of *M. oeconomus* (or at least closely related to the ancestral form) in early-mid Pleistocene deposits on the Seward Peninsula in Alaska. This fossil species is closely related to *M. paroparins,* a common vole from deposits of Kansan age in the Great Plains (PAULSON, 1961). The presence of the fossil species allows us to look at the variability patterns with a direct knowledge of the parts that are the most phylogenetically stable and those

Fig. 3. Heritability estimates for several measurements the dental surfaces of *Microtus oeconomus* from Fairbanks, Alaska. Sireson regressions were used with a sample size of 50. Standard errors clustered around ± .25

that are the most labile in this particular line. The M_3 and M^3 show the greatest difference. The heritability estimate of stable areas is around the same magnitude as the heritability estimate of the rapidly changing areas. The high error of the estimate precludes any detailed analysis of this relationship.
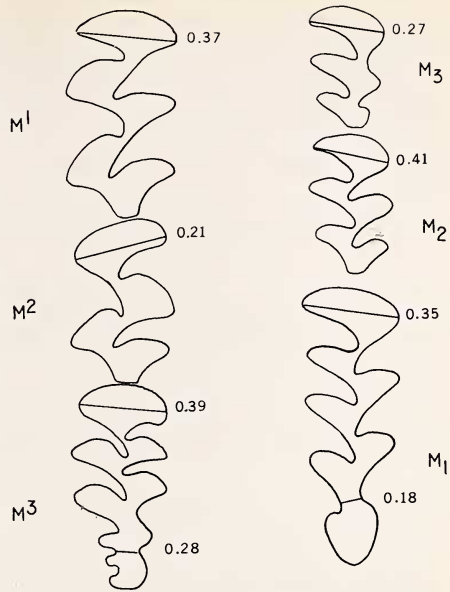
The Stein—Zimmerman controversy

There have been a number of disagreements over specific explanations of patterns of microtine tooth variations, but the one most publicized has been the problem of the north-south cline in the M^3 of *Microtus arvalis*. STEIN (1931) originally established the geographical features of the M^3 variations. He found that the northern forms had a much higher incidence of what was called the *simplex* form (only three inner foldings or salient angles) than those subspecies in the south. ZIMMERMAN (1935) later confirmed this cline in a study using larger collections and more samples.

ZIMMERMAN in a later study (1953) showed that a component of the molar variation in *Microtus arvalis* was genetic. He proposed that the cline represented an accumulation of a recessive on the periphery of the species' range, and questioned the idea that either the *simplex* or the *complex* has any selective advantage. Moreover, he regarded the phenomenon as an intermediate stage in the simplification of microtine dentition. Here, he was following HINTON's early misinterpretation of the trends found from microtine fossil record. Later evidence from the fossil record has shown that the overall pattern is an increase, rather than a decrease, in complexity. (This fact is not critical to ZIMMERMANNs explanation since it only changes the direction of the evolution.)

In a later work STEIN (1958) proposed his balanced polymorphism theory to

explain the cline in the variation of M³. He argued that the *simplex* M³ has a selective advantage in a poor environment and since the climate in Eurasia is more favorable in the *simplex* is least abundant there and most abundant in the north. He supports his idea with samples of *Microtus arvalis* from quite different ecological situations. Those populations in woodlands (STEINS category of poor *Microtus* habitat) have a significantly higher percentage of *simplex* tooth than nearby populations in meadow grassland.

In ZIMMERMANS (1958) rejoinder to STEINS theory he argued that there are a number of places where the populations of *Microtus arvalis* have predominantly *simplex* M³'s, yet the conditions that they live under could not be thought of as being poor. His other criticism of STEINS idea was based on the lack of increase of *simplex* M³'s under poor conditions (a high winter-kill). ZIMMERMAN went on to explain the higher occurrence of the *simplex* tooth form in woodlands by contending that a greater degree of inbreeding occurs there.

According to the theory of forces regulating microtine tooth complexity that I have presented in this study, there would be two possible explanations for the *Microtus arvalis* molar cline: (1) the demands of the food itself, and (2) intracommunity pressures, that is, the difference in competition between distantly related forms (genera) or between closely related forms (species).

The weak points of the first explanation, that it is simply a selection by the food for *simplex* teeth in the north and *complex* teeth in the south, have been pointed out by ZIMMERMAN. One might expect that the frequency of complex teeth might increase as the general distribution of a species of *Microtus* is traced from woodland to grassland. (The east-west complexity gradient of *M. pennsylvanicus* [SEMKEN, 1966] accompanying the gradient of woodland-grassland might be explained in this way). However, there seems to be not obvious vegetational gradient of this nature which accompanies the cline in the southern decrease in the frequency of *simplex* M³ in *Microtus arvalis*. STEINS theory may be valid for the differences in M ³ pattern found in different local environments. Perhaps one reason the areas with high overhead cover are the primary habitat of *Clethrionomys* is that not only does it have cover, but this is the area the fruiting plant parts, which it prefers, are relatively more common. Therefore, one can see that among the individuals of *Microtus* which invade the woodlands, those with simpler teeth (which are better for crushing than grinding) will fare the best, whereas in the meadows the reverse would be true. Significantly, there also seems to be a cline in tooth complexity of *Clethrionomys glareolus* with the frequency of the *simplex* also decreasing toward southern Europe.

The findings by REICHSTEIN and REISE (1965) also suggest that there may be some general vegetational factor since another species of *Microtus (M. agrestis)* has some dental variations that are simpler in northwestern Germany and Denmark, the very areas where *M. arvalis* are found with simple tooth patterns.

The second alternative is to propose that the cline in tooth complexity is due to competition with other genera. Throughout the distribution of *Microtus arvalis*, the most likely candidate would be *Clethrionomys*. There are three main species involved. *Clethrionomys glareolus* is the most dominant member within the distribution of *Microtus arvalis;* however, if this species of *Clethrionomys* competed differently in the north than in the south one would expect a complemntary reversed cline in the tooth complexity of it. No evidence has as yet been presented that this pattern does exist. In actuality the cline, if any exists it is quite ragged, in *Clethrionomys glareolus*, runs the same direction that it does in *Microtus arvalis*.

The other two species, *Clethrionomys rutilus* and *Clethrionomys rufocanus*, do overlap with *M. arvalis* somewhat in western Asia and eastern Europe (OGNEV, 1950), in precisely those areas where the frequency of *simplex* is the highest. However, this

does not account for cline in tooth complexity in the other parts of the distribution of *Microtus arvalis*. For example, in western Europe the *simplex* form reaches 90 % without either *Clethrionomys rutilus* or *Clethrionomys rufocanus* being present. So it looks as if intergeneric competition cannot as yet be used as a complete explanation of the *Microtus arvalis* tooth cline; although, it may be one of the contributing factors.

In western Europe the higher frequency of *simplex* toward the north might be explained by increasing competition with a northern species with more complex teeth. But, as I mentioned earlier, *M. agrestis* seems to also have simpler teeth in somewhat the same area as *M. arvalis*.

Obviously, a lot more ecological information will be needed before any decisive analysis can be made, but these hypotheses, based on factors regulating dental complexity in other situations, may prove to be fruitful avenues of investigation.

Some implications of microtine tooth variations to general evolutionary theory

The variation patterns found among modern and fossil microtines do not upset any current evolutionary concepts; they do, however, clarify some features. The overall microtine radiation pattern is what evolutionists have referred to as grade evolution, where new forms continue to originate in a directional "progression". These sequence of grades can take place at any taxonomic level. In microtines it is primarily a generic grade. Since the cricetines already occupied the fruit-seed-eating niches, the mircotine radiation involved the acquisition of an adaptive complex which allowed them to exploit other portions of plants. As long as the other niches are occupied, the only radiation route available was to increase tooth complexity. Microtine grade evolution is probably not a progression of successive jumps into pre-established quantum categories, but a diversification that is forced to have an orientation because competition excludes all possible routes except one, or at least has an unidirectional orientation. The directional component of many other radiations of this nature also seems to be chiefly controlled by intercommunity competition, where further exploitation can only occur away from the baseline (successive niche displacement). As each new specialization materializes, the „ante" is increased so that new exploitation must move even farther. Rather than thinking of directional trends affecting one isolated line through time, it is probably closer to reality to think of the community diversifying unidirectionally.

Another contribution of mircotine studies to evolutionary thought concerns the relation of variation and niche width. As others have found, pressures from *stabilizing* selection seem to be the main factor regulating intrapopulational variation. From our comparisons of insular populations of one species to the same species on the mainland in a much more heterogeneous community, we can conclude that community pressures keep a species from broadening its utilization of the entire potential food source, with the consequence that success of the morphological (and presumably physiological and behavioral) varients able to operate in the perimeter of the potential is poor. Without these pressures (on an island, say) the population tends to move toward the mean best able to utilize the most common food source. When a population is taken out of the original community context this usually results in reversing down the scale (with the possible exception of those members that have been forced to hug the baseline in a complex community).

Within the framework of the "grade" model, it is easy to see how the successive stacking of species diversity through competition from above results in a niche compression all down along the line (Fig. 4). The earliest types that once occupied a broad
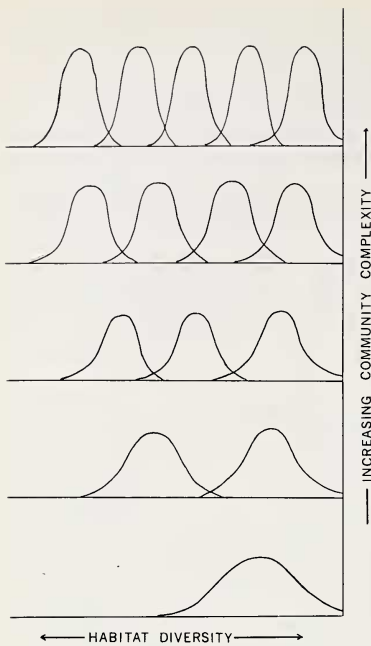
Fig. 4. Diagram of the "stacking phenomenon", the theoretical effect of increasing community complexity on species variations, and the partitionig of the available habitat

habitat range are now pushed into a very specialized existence or have become extinct. I mentioned earlier in the paper how the earlier types in a grade pattern now exist only in quite specialized areas or niches (e. g., Pottos and lorises among the primates, and microtines with rooted molars).

The selection feedback from other populations in the community throws some light on ideas of inter-group selection. The direction of possible evolution of one group is certainly influenced by the others. If one group becomes extinct, the others are directly affected. However, this technically is not group selection, since the actual mechanics of the original changes and the subtle shift and balances that continue to take place are products of selection at the individual level.

The mechanics of the regulation of microtine dental variability and complexity can be accounted for simply by Darwinian selection (selection within the population). In a complex community of many species the individuals who, because of dental morphology or some other features, were in greater competition with other species than were other members of their own species, would be expected to leave fewer offspring to the next generation, all else being equal.

Summary

This is an attempt to investigate the more theoretical aspects of a recent radiation and to assess the relationships between the community influences and the strict physical adaptations to diet.

Like that of the mammoths, the microtine radiation occurred rather late, much later apparently than the origin of the general habitat which they now occupy. I have proposed that the phylogenetic distance was an important factor in the evolutionary lag. Because of this late blossoming of their radiation, microtines have had one of the most rapid evolutionary rates among mammals.

A new model is presented to account for the evolution and regulation of microtine tooth complexity. The interpopulational variation, the intrapopulational variation, and the nature of microtine dental patterns seem to be determined mainly by the existing community structure of microtine species or related (phylogenetically or ecologically) forms. The direction of the microtine radition was a product of only one broad dietary avenue being available for exploitation. Thus, the history of microtine communities builds in complexity from a baseline of fruit-seed eating toward the coarser plant parts. Decreasing the complexity of a microtine community by either artificial or natural means (islands) causes the remaining species so shift their variation toward the average morphology of the missing species. I have generalized this whole phenomenon by suggesting that a major factor in the orientation of many evolutionary trends, which persist for a long period of time in a radiation, may be a product of the community structure as well as exploitation of a new resource.

Zusammenfassung

Folgendes Denkmodell zur Erklärung der Evolution und Regulation der Komplexizität der Microtinen-Molaren wird vorgetragen: die rasche Evolution der Molarenstruktur der Wühlmäuse steht in einem engen Zusammenhang mit der Erschließung neuer Nahrungsquellen: an die Stelle der Ernährung durch Früchte und Samen trat die Ernährung durch vegetative Pflanzenteile. Die Vielgestaltigkeit des Zahnschlingenmusters — die Variabilität innerhalb und zwischen den Populationen — wird gedeutet als Folge interspezifischer und intergenerischer Konkurrenz, wobei der Nahrung selbst auch ein unmittelbarer Einfluß zugeschrieben wird.

Acknowledgements

Literature

BADER, R. S. (1965): Heritability of dental characters in the house mouse. Evol. **19**, 378—384.

BEE, J. W., and HALL, E. R. (1956): Mammals of northern Alaska on the arctic slope. Univ. of Kansas Mus. Nat. Hist. Misc. Publ. 8. 309 p.

CAMERON, A. W. (1964): Competitive exclusion between rodent general *Microtus* and *Clethrionomys*. Evol. **18**, 630—634.

CHITTY, D., and PHIPPS, E. (1966): Seasonal changes in survival in mixed populations of two species of vole. J. Anim. Ecol. **35**, 313—331.

CORBET, G. B. (1963): An isolated population of bank vole *Clethrionomys glareolus* with aberrant dental pattern. Proc. Zool. Soc. London **140**, 315—319.

— (1964): Regional variation in the bank vole *Clethrionomys glareolus* in the British Isles. Proc. Zool. Soc. London **141**, 191—219.

— (1966): The terrestrial mammals of western Europe. G. T. Foulis, London. 264 p.

FALCONER, D. S. (1960): Introduction to quantitive genetics. Ronald Press, New York. 365 p.

FINDLEY, J. S. (1954): Competition as a possible limiting factor in the distribution of *Microtus*. Ecol. **35**, 418—420.

FOSTER, J. B. (1963): The evolution of the native land mammals on the Queen Charlotte Islands an the problems of insulanity. Ph. D. thesis. Univ. of British Columbia, Vancouver.

GRANT, P. R. (1965): The adaptive significance of some size trends in island birds. Evol. **19**, 355—367.

GUTHRIE, R. D. (1965): Variability in characters undergoing rapid evolution, an analysis of *Microtus* molars. Evol. **19**, 214—233.

— (1969): Paleoecology of a late Pleistocene small mammal community from interior Alaska. Arctic **21**, 223—244.

GUTHRIE, R. D., and MATTHEWS, J. V. (Unpublished manuscript): First early Pleistocene mammalian fauna form the Arctic.

HIBBARD, C. W. (1959): Late Cenozoic microtine rodents from Wyoming and Idaho. Pap. Mich. Acad. Sci., Arts, and Letters **44**, 3—40.

— (1964): A contribution to the Saw Rock Canyon local fauna of Kansas. Pap. Mich. Acad. Sci., Arts, and Letters **49**, 115—127.

HIBBARD, C. W., and ZAKRZEWSKI, R. J. (1967): Phyletic trends in the late Cenozoic microtine *Ophiomys* gen NOV., from Idaho. Contr.Mus. Paleo., Univ. Michigan **21**, 255—271.

HINTON, M. A. C. (1926): Monographs of the voles and lemmings (microtine) living and extinct. British Mus. Nat. Hist., London. 488 p.

HOPKINS, D. M. (1959): Cenozoic history of the Bering Land Bridge. Science **129**, 1519—1528.

KOPLIN, J. R., and HOFFMAN, R. S. (1968): Habitat overlap and competitive exclusion in voles *(Microtus)*. Amer. Midl. Nat. **80**, 494—507.

KOWALSKI, K. (1966): The stratigraphic importance of rodents in the studies on the European Quaternary. Folia Quaternania Nr. 22. 16 p.

KURTÉN, B. (1960): Chronology and faunal evolutions of the earlier European glaciations. Societas Scientiarum Fenica Commentationes Biologica **21**, 1—62.

Leamy, L. J., and Bader, R. S. (1968): Components of variance of odontometric traits in a wild-derived population of *Peromyscus leucopus*. Evol. 22, 826—834.

Ognev, S. I. (1950): Mammals of the USSR and adjacent countries. Vol. 7, Rodents, Israel Program for Scientific Translations, Ltd., Jerusalem, 1964. 626 p.

Paulson, R. G. (1961): The mammals of the Cudahy fauna. Pap. Mich. Acad. Sci., Arts, and Letters 46, 127—153.

Pitelka, F. A. (1957): Some characteristics of microtine cycles in the Arctic, pp. 73—78, in: Arctic Biology; 18th Annual Biological Colloquium, Oregon State College, Corvallis.

Pruitt, W. O. Jr. (1966): Ecology of the terrestrial mammals. pp. 355—362, in: Environment of the Cape Thompson Region, Alaska; by N. J. Wilimowski (ed.), N. J. Wolfe (assoc. ed.), U. S. Atomic Energy Commission, Oak Ridge.

Rausch, R. L. (1951): Notes on the Nunamiut Eskimos and mammals of the Anaktuvuk Pass region, Brooks Range, Alaska. Arctic 4, 147—195.

Rausch, R. L., and Rausch, V. R. (1968): On the biology and systematic position of *Microtus abbreviatus* Miller, a vole endemic to the St. Matthew Islands, Bering Sea. Z. Säugetierkunde 33, 65—99.

Reichstein, H., and Reise, D. (1965): Zur Variabilität des Molaren-Schmelzschlingenmusters der Erdmaus *Microtus agrestis* Z. Z. Säugetierkunde 30, 36—47.

Selander, R. K. (1966): Sexual dimorphism and differential niche utilizations in birds. Condor 68, 113—151.

Semken, H. A. (1966): Stratigraphy and paleontology of the McPherson Equus beds (Sandahl local fauna), McPherson County, Kansas. Contr. Mus. Paleo., Univ. Michigan 20, 121—178.

Stein, G. H. W. (1931): Beiträge zur Kenntnis einiger mitteleuop. Säuger. Mitt. Zool. Mus. Berlin 17, 27—34.

— (1958): Über den Selektionswert der simplex-Zahnform bei der Feldmaus *Microtus arvalis* (Pallus). Zool. J. Syst. 86, 27—34.

Steven, D. M. (1953): Recent evolution in the genus *Clethrionomys*. Symp. Soc. Exp. Biol. 7, 310—319.

Van Valen, L. (1965): Morphological variation and width of ecological niche. Amer. Nat. 99, 377—390.

Wilson, E. O. (1956): Character displacement and species criteria. Proc. 10th Inter. Congr. Entom. 1, 125—128.

Zimmerman, E. G. (1965): A comparison of habitat and food of two species of *Microtus*. J. Mammal. 46, 605—611.

Zimmermann, K. (1935): Zur Rassenanalyse der mitteleuropäischen Feldmaus. Arch. Naturgesch. N. F. 4.

— (1953): Die simplex-Zahnform der Feldmaus *Microtus arvalis* (Pallus). Verh. Dtsch. Zool. Ges. Freiburg, 1952, 492—498.

— (1956): Zur Evolution der Molar-Strukur der Erdmaus, *Microtus argestis* (L.). Zool. Jb. Syst. 84, 269—274.

— (1958): Selektionswert der simplex-Zahnform bei der Feldmaus. (Eine Entgegnung). Zool. Jb. Syst. 86, 35—40.

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